Oecologia (2004) 141: 687–700
DOI 10.1007/s00442-004-1684-2

COMMUNITY ECOLOGY

Scott A. Mangan · Ahn-Heum Eom · Gregory H. Adler · Joseph B. Yavitt · Edward A. Herre

Diversity of arbuscular mycorrhizal fungi across a fragmented forest in Panama: insular spore communities differ from mainland communities

Received: 13 February 2004 / Accepted: 9 July 2004 / Published online: 19 August 2004

Abstract It is now understood that alterations in the species composition of soil organisms can lead to changes in aboveground communities. In this study, we assessed the importance of spatial scale and forest size on changes in arbuscular mycorrhizal fungal (AMF) spore communities by sampling AMF spores in soils of forested mainland and island sites in the vicinity of Gatun Lake, Republic of Panama. We encountered a total of 27 AMF species or morphospecies, with 17, 8, 1 and 1 from the genera *Glomus*, *Acaulospora*, *Sclerosystis*, and *Scutellospora*, respectively. At small scales (<100 m^2), we found little evidence for spatial structuring of AMF communities (decay of Morisita-Horn community similarity with distance). However, at large spatial scales, we found that the AMF spore community of a mainland plot was more similar to other mainland plots several kilometers (>5) away than to nearby island plots (within 0.7 km). Likewise, most island plots were more similar to other island plots regardless of geographic separation. There was no decay in AMF species richness (number of species), or Shannon diversity (number of species and their spore numbers) either with decreasing forest-fragment size, or with decreasing plant species richness. Of the six most common species that composed almost 70% of the total spore volume, spores of *Glomus* "tsh" and *G. clavisporum* were more common in soils of mainland plots, while spores of *Glomus* "small brown" and *Acaulospora mellea* were more abundant in soils of island plots. None of these common AMF species showed significant associations with soil chemistry or plant diversity. We suggest that the convergence of common species found in AMF spore communities in soils of similar forest sizes was a result of forest fragmentation. Habitat-dependent convergence of AMF spore communities may result in differential survival of tree seedlings regenerating on islands versus mainland.

Keywords Fungal spores · Species diversity · Community assemblage · Forest fragmentation

S. A. Mangan (✉)
Department of Biology, Indiana University,
Bloomington, IN, 47405, USA
e-mail: smangan@indiana.edu
Fax: +1-812-8556705

S. A. Mangan · A.-H. Eom · E. A. Herre
Smithsonian Tropical Research Institute,
Apartado 2072,
2072 Balboa, Republic of Panama

A.-H. Eom
Institute of Natural Science, Korea National University of Education,
Chungbuck, 363-791, Republic of Korea

G. H. Adler
Department of Biology, University of Wisconsin,
Oshkosh, WI, 54901, USA

J. B. Yavitt
Department of Natural Resources, Cornell University,
Ithaca, NY, 14853, USA

Introduction

Determining how biological communities are assembled and the factors that influence species distributions are fundamental challenges in ecology. Numerous empirical studies have been conducted to test proposed mechanisms for the maintenance of species diversity (e.g., island biogeography, predation, density-dependence, and competition). Historically, these studies have been largely concentrated on macroorganisms that occur aboveground (e.g., trees, insects, birds, and mammals). Recently, however, there has been a strong call to characterize communities of belowground microorganisms (e.g., soil fungi, nematodes, and bacteria). Such organisms have been shown to directly and indirectly influence the ecologies of plants, animals, and microbes (van der Putten et al. 2001; Reynolds et al. 2003). Furthermore, theories on species diversity and distribution developed for larger aboveground organisms may not apply to microscopic organisms, particularly those living in viscous environments such as soil.

The importance of soil organisms, particularly soil fungi, in shaping the distribution and diversity of plant communities is only now being appreciated (Bever 1994; Mills and Bever 1998; van der Heijden et al. 1998a; Olff et al. 2000; Kiers et al. 2000; Klironomos 2003; Castelli and Casper 2003). For example, species-specific fungal pathogens appear to promote species diversity of plants by limiting recruitment of conspecific seedlings near parent plants, thus providing opportunities for rarer species to recruit (Augspurger 1984; Gilbert et al. 1994; Mills and Bever 1998). The importance of density-dependent mortality for the maintenance of diverse plant communities is now recognized both in neotropical (Wills et al. 1997; Harms et al. 2000) and temperate forests (Packer and Clay 2000; Lambers et al. 2002).

Studies investigating the ecological importance of beneficial fungi such as arbuscular mycorrhizal fungi (AMF) are in their infancy. However, available results suggest that AMF also are important in influencing diversity and distribution of plant communities (Gange et al. 1993; van der Heijden et al. 1998b; Hartnett and Wilson 1999). AMF colonize roots and subsequently provide plants with the increased ability to take up scarce nutrients (Sanders and Koide 1994), resulting in increased growth, drought tolerance, and protection against disease. In return, AMF are obligately dependent on plants for carbohydrates. Pot experiments show that different species of AMF clearly invoke different growth responses of individuals within a plant species (Mosse 1972; Nemec 1978; Schenck and Smith 1982; Streitwolf-Engel et al. 1997; van der Heijden et al. 1998b; Bever 2002; Klironomos 2003; Eom et al. submitted). Furthermore, different AMF species differentially associate with roots of different host species (Helgason et al. 2002; Husband et al. 2002). Moreover, a given AMF species exhibits distinctly different patterns of spore production (sporulation) depending on the species of plant colonized (Johnson et al. 1992; Sanders and Fitter 1992; Bever et al. 1996; Eom et al. 2000). Such differences in spore production, coupled with differential growth promotion and host association across AMF and plant species, may increase plant diversity through both niche diversification (van der Heijden 1998a) and negative feedback (Kiers et al. 2000; Bever 2002; Castelli and Casper 2003).

In Neotropical forests, AMF are common and are associated with a large proportion of plant species (Janos 1980; Siqueira et al. 1998; Zangaro et al. 2003). To date, the majority of studies examining the composition of AMF communities in the neotropics have concentrated on comparing AMF spore composition in soils of intact forests to those in adjacent disturbed soils such as pasture (Fischer et al. 1994; Johnson and Wedin 1997; Allen et al. 1998; Picone 2000). Although differences in AMF-spore communities are often detected, such studies compare AMF-spore abundances associated with very different types of hosts (e.g., grasses vs trees) where differences in AMF spore communities are perhaps no surprise (but see Picone 2000). However, it is unknown whether more subtle changes in host communities (or microclimates), such as those following forest isolation, promote detectable changes in AMF-spore communities. Furthermore, little is known about the spatial scales in which changes in AMF communities can be detected in neotropical forests (Janos 1992). Such scales may differ from those of their aboveground counterparts because AMF propagules are relatively small (40–350 μm) and reside in a viscous environment (i.e., soil). Although spores of some AMF species have evolved long-distance dispersal by small mammals (Gerdemann and Trappe 1974; Janos et al. 1995; Mangan and Adler 2002), dispersal of spores from soil surrounding the host root system is thought to be limited for the majority of AMF species. Indeed, such dispersal limitation is likely to explain why AMF spore communities are often spatially structured at fine scales in temperate soils (Bever et al. 1996; Pringle and Bever 2002).

Low AMF spore counts in tropical soils found in earlier studies suggested that this inoculum source was unimportant to future colonization when compared with other AMF inocula sources (e.g., hypha; Janos 1992). However, recent studies have revealed that spores are abundant in soils of many tropical forests (Johnson and Wedin 1997; Picone 2000), and spores of some AMF genera are the only source of inoculum for the colonization of host plants (Hart and Reader 2002). Thus, the importance of the species composition and distribution of AMF spores cannot be ignored.

In this paper, we examined the distribution of AMF spores in soils of both forested mainland and islands in Gatun Lake, Panama. Our primary objective was to search for patterns of AMF-spore composition across different forested sites with respect to forest-fragment size (island or mainland) and geographic locations. We thus focused on the scales over which AMF communities may vary. Specifically, (1) Are AMF-spore communities more similar among forest patches within close geographic proximity, or are communities more similar in soils of forest patches of similar size? (2) Are AMF-spore communities more similar among soil samples collected within a 9×9-m plot than to soil samples collected at random over larger scales? and (3) Are AMF-spore communities spatially structured at fine scales? We also investigated whether edaphic characteristics and plant diversity were correlated with AMF community composition.

Materials and methods

Study system

This study was conducted in lowland, moist forest in the Barro Colorado Nature Monument (BCNM), Panama. This region of the Neotropics is subjected to highly seasonal rainfall, with <10% of the annual precipitation (~2,600 mm) falling from January to April (Windsor 1990). During construction of the Panama Canal (~1,910),

over 200 hilltops were isolated as islands by damming the Chagres River to form Gatun Lake.

Today, most of the small islands (<0.5–3.5 ha) of Gatun Lake are covered completely by secondary forest (Adler 2000). These forest fragments have reduced tree-species diversity and are more likely to share common species than in similar-sized patches within forest of the mainland (Leigh et al. 1993). Increased edge-to-interior ratio of forest fragments can dramatically alter microclimates and increase the susceptibility of interior species to disturbance by wind. Furthermore, seed dispersers and pollinators may be unwilling to cross water to reach small forested islands. These factors, in part, are presumed to have led to both the decay of tree-species diversity and the shift in tree-species composition on small islands of Gatun Lake (Leigh et al. 1993). Whether soil organisms follow similar patterns of altered community composition following isolation remains unexplored.

Sampling design

In December 1999, nine study plots were established on islands and adjacent mainland of the BCNM. Plots were located in three geographically distinct groups, with each group separated by a minimum of 5 km. Each geographic group (labeled 12, 51, and 53; see Fig. 1) contained three plots, with each plot located in forest patches of different size: one plot was located on the mainland (Main), one plot was located on a medium-sized island (1.8–3.5 ha, MI), and one plot was located on a small island (<0.5 ha, SI; Fig. 1). Plots on both mainland and islands were located at a similar distance from the shoreline so that plots were located at similar elevation and exposed to similar edge effects. The maximum distance between any two island or mainland plots within a geographic group was no more than 0.7 km. Each study plot contained a 9×9-m grid consisting of 16 sampling points, with points spaced 3 m apart.

At each of the 16 sampling points per study plot, we collected and combined three 250-g soil cores collected from a depth of 0–10 cm. Soil collected from each sampling point was sieved to remove large roots and then thoroughly homogenized. AMF spores were extracted using wet sieving and sucrose density-gradient centrifugation (Daniels and Skipper 1982), identified and counted from 5-g samples. For AMF spores not previously described, morphospecies labels were given. Samples used for assessing AMF composition at each sampling point were formed by subsampling the homogenized soil a minimum of ten times or until a 5-g sample was formed. Fresh soil (50 g) from each sampling point per plot was

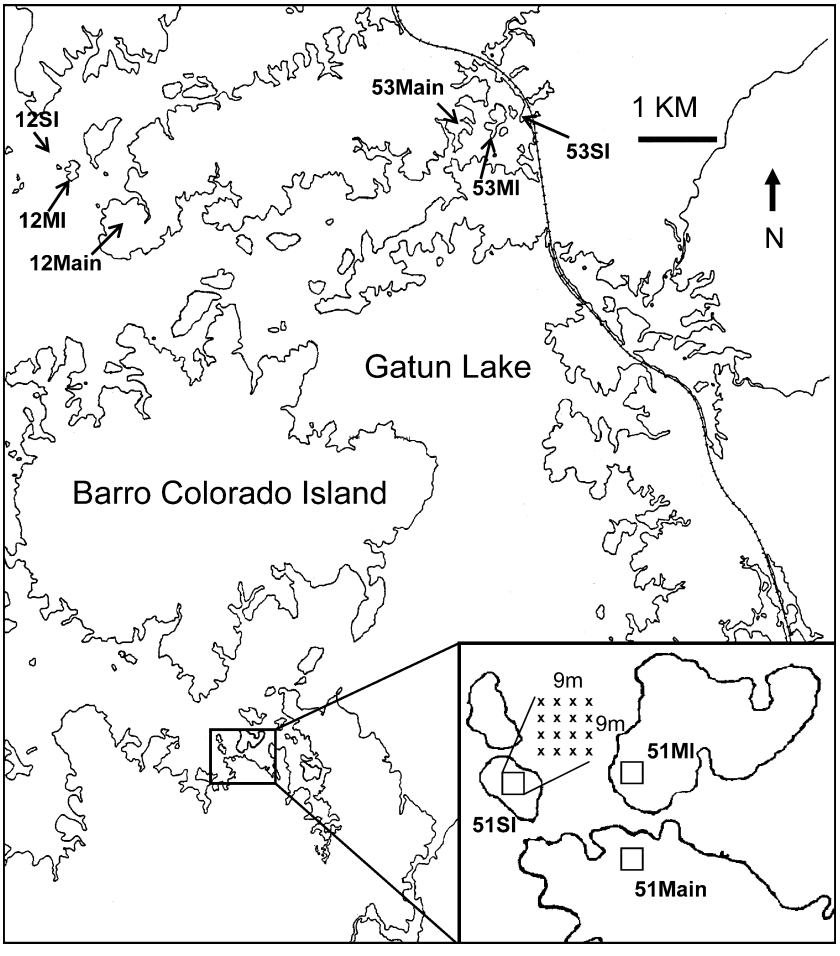

Fig. 1 Map of the BCNM showing the location of each geographic group and forest-fragment size. Numbers assigned to each geographic group correspond to the medium size islands as presented in Mangan and Adler (2002). The *inset* illustrates the design of the 16 sampling points per study plot

dried to determine percent soil moisture. Three soil cores collected randomly over each 9×9-m plot were homogenized and analyzed for Al, Ca, P, NH_4, and NO_3 (see Yavitt 2000 for methods).

Vegetation sampling

To characterize the plant species composition of the forest within and surrounding each 9×9-m sampling plot, we marked, measured, and identified all trees ≥10 cm diameter at breast height (DBH) located in the 30×30-m area encompassing each plot. In addition, all plant stems ≥0.5 m in height within and 1 m around the 9×9-m sampling plot were identified, tagged, and mapped.

Statistical analyses

AMF spore community composition

AMF community similarity across 9× 9-m plots We began the analysis of AMF community composition by examining AMF-species similarity across the three forest-fragment sizes and the three geographic groups at the whole-plot level. Spore counts from each of the 16 sampling points per 9×9-m sampling plot were pooled (separately for each AMF species) and used as the abundance measure in estimating community similarity across the nine sampling plots, with each 9×9-m plot as the sampling unit. Community similarity was estimated in two ways to investigate the relative importance of spore abundance and species presence and absence on patterns of AMF community similarity. We first computed Morisita-Horn similarity indices for all possible pair-wise comparisons among the nine sampling plots to examine the influence of both species identity and abundance of spores on AMF community similarity. Jaccard similarity indices were also computed to examine the importance of only species presence or absence on AMF community similarity. We computed all similarity indices using EstimateS (version 6b1a; Colwell 1997). Unweighted pair-group cluster analysis using the clustering program NYSTS (version 2.10p) was performed using the two similarity estimates separately and dendrograms were constructed to examine potential patterns in similarity among the sampling plots.

AMF community similarity across sampling points We explored how AMF communities at single sampling points varied over different spatial scales. Specifically, were AMF communities at sampling points more similar within each plot than to AMF communities at sampling points sampled over broader scales? We used randomization to test the null hypothesis that AMF communities at each sampling point were uniformly distributed across all study plots. We estimated AMF community similarity within each plot by computing Morisita-Horn similarities for all possible pair-wise comparisons of the 16 sampling points per plot (total number of possible comparisons =120). For each plot, the 120 indices were averaged, and this mean was used as an index of "within-plot similarity". We then generated a list of similarity indices computed for all possible pair-wise combinations of all 144 sampling points contained within the nine study plots. This list was shuffled randomly, and a mean was computed for the first 120 indices. This process was repeated 10,000 times, thus generating a frequency distribution (null distribution) of randomly generated means that was normally distributed, with the mean of the distribution representing the "global AMF similarity" of our study site. To determine whether "within-plot-similarity" of each of the study plots was significantly greater than "global AMF similarity" (thus rejecting the null hypothesis), we calculated the probability that each "within-plot similarity" index fell outside the right tail of the null distribution.

Next, we repeated the randomization procedure to determine whether Morisita-Horn similarity of AMF communities of sampling points within each plot was greater than similarity of AMF communities within that plot's associated forest-fragment size and geographic group. We generated null distributions for each forest-fragment size (e.g., all sampling points within the three plots located on the mainland) and for each geographic group (e.g., all sampling points within the three plots located in geographic group "12"). Six null distributions were generated in total. Probabilities were computed to test the null hypothesis that "within-plot similarity" of each plot did not differ from each plot's respective forest size and geographic group null means.

Finally, we used the initial null distribution (the distribution created by comparing all possible pair-wise combinations across the sampling site) to determine whether AMF communities at sampling points contained within each forest-fragment size and within each geographic group were more similar than sampling points selected at random. For AMF communities at sampling points contained within each forest-fragment size and within each geographic group (48 sampling points per fragment size or geographic group), we computed Morisita-Horn similarities of all possible pair-wise combinations. Probabilities were then computed to determine whether each of the six resulting means (three "within forest-fragment size" and three "within geographic group") was greater than the global AMF mean.

AMF community similarity and distance within a 9× 9-m plot We used randomization and linear regression to investigate the extent of spatial structure of the AMF community of each study plot. Morisita-Horn and Jaccard similarities were computed for each pair-wise combination of spore communities of sampling points within a plot, and distance between sampling points of each pair was calculated. Therefore, for each plot, a list of similarity indices and associated distances was generated. We first examined whether similarities of sampling points within closest proximity (i.e., 3 m) were significantly greater than "within-plot similarity" by generating separate frequency

distributions per plot as described above. To determine whether community similarity decayed linearly with distance, we computed mean similarity for each possible distance and used linear regression to explore possible relationships between mean similarity and distance separately for each plot.

Response of individual AMF species to geographic location and fragment size

The influence of geographic group and forest-fragment size on spore abundance was examined using multivariate analysis of variance (MANOVA). AMF species that occurred in at least six of the nine plots, and in at least 20% of the 144 sampling points were included in the analysis (Johnson and Wedin 1997). Spore number for each AMF species was converted to ranks across the data set. Both geographic location and forest-fragment size (and their interaction term) were included in the MANOVA as independent variables, and rank spore number was included as the dependent variable. Overall effects were assessed by examining Wilks' Lambdas and their associated approximate *F*-ratios. Next, we used two-way mixed-model analysis of variance (ANOVA) to examine the importance of geographic group and forest-fragment size on mean spore ranks (separately for each AMF species) in each of the 16 sampling locations per sampling plot. For each model, geographic group and its interaction with forest-fragment size were included as random effects, while forest-fragment size was included as a fixed effect. MANOVA and mixed-model ANOVAs were performed using PROC GLM in SAS (SAS 1996)

Influence of soil characteristics and vegetation on spore abundance

Spearman rank correlation coefficients were computed to examine potential relationships among percent soil moisture, soil nutrients, AMF diversity, and plant diversity. We estimated alpha diversity of AMF in soils of each 9×9-m plot in two ways. First, the total number of AMF species found in each plot (i.e., species richness) was calculated. Also, Shannon diversity of AMF was calculated by including the relative proportion of total spore volume (of all plots) of each AMF species found in each plot as the abundance measure. Likewise, we computed species richness and Fisher's alpha diversity (Leigh 1999, p 179) for all stems ≥0.5 m in height within each 9×9-m plot and for all trees ≥10 cm DBH of the 30×30-m area encompassing each plot.

Results

AMF spore community composition

Spores of 27 AMF species or morphospecies were identified, including 8 from the genus *Acaulospora*, 17 from the genus *Glomus*, 1 species of *Sclerosystis*, and 1 species of *Scutellospora* (Appendix). Six species constituted almost 70% of the total spore volume. Both *Glomus* "tsh" and *Glomus* "small brown" were the most abundant, each contributing approximately 19% of total spore volume. *Acaulospora foveata*, *A. mellea*, *Glomus* "8", and *G. clavisporum* constituted the remaining 70% of total spore volume (see Appendix for the remaining AMF species).

AMF community similarity across 9× 9 m plots

Despite large geographic separation (Fig. 1), AMF communities were more similar among mainland than among island plots located in the same geographic group. For example, the AMF community of a mainland plot was more similar to mainland plots ≥5.0 km away than to island plots within 0.7 km close proximity. Likewise, island plots were more similar to island plots than to mainland plots. Cluster analysis of Morisita-Horn similarity indices revealed two distinct clusters; one cluster contained only mainland plots, while most island plots composed the second cluster (Fig. 2). However, the second cluster did not discriminate between small- or medium-sized islands. Community similarity was largely explained by changes in patterns of species abundance (i.e., AMF species richness and spore abundance) and not solely by species identity. When the Jaccard index (only species presence and absence) was used to measure AMF community similarity, no apparent clustering by either fragment size or geographic group occurred (Fig. 2).

AMF community similarity across sampling points

In general, AMF community structure was hierarchical according to scale, with community similarity being highest among sampling points within each 9×9-m study plot and lowest among sampling points selected at random over the largest scale ("global AMF similarity"). Only plots 12MI and 53SI had "within-plot similarity" no higher than "global AMF similarity" (Fig. 3a, Table 1). AMF community similarity among sampling points within a study plot was higher than similarities calculated among sampling points selected at random within plots of similar forest-fragment size (five of the nine plots were significant) and within plots of similar geographic location (six of the nine plots were significant).

When community similarity among sampling points contained within each forest fragment size or within each geographic group was examined, sampling points located within plots of the same forest-fragment size had

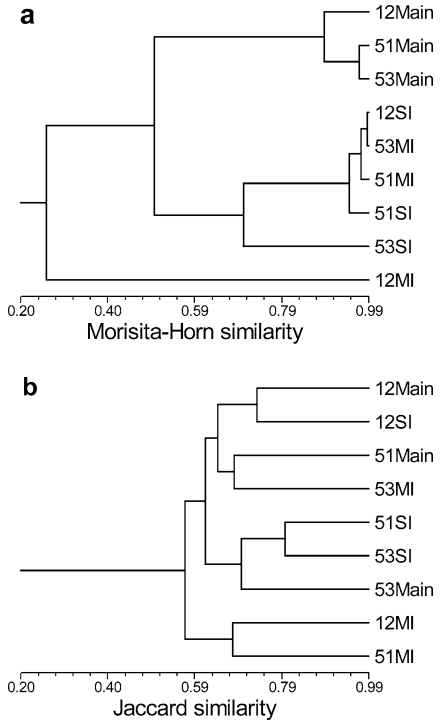

Fig. 2a, b Dendrograms illustrating AMF-community similarity among mainland (*Main*), medium-sized island (*MI*), and small-sized island (*SI*). Cluster analyses were conducted both on Morista-Horn similarity indices (species presence and spore abundance; **a**) and on Jaccard similarity indices (species presence; **b**)

Table 1 *P*-values indicating significance of separation of mean Morisitia-Horn similarities of each of the nine plots (i.e., "within-plot similarity") from mean similarity of all sites combined (i.e., "global AMF similarity"; Fig. 2a), from mean similarity of each plot's respective forest-fragment size, and from mean similarity of each plot's respective geographic group. Means for each forest-fragment size and geographic group are shown in Fig. 2b. $P \leq 0.05$ indicates a mean significantly greater than the global AMF mean or a mean greater than a forest-fragment size or geographic mean

	Global AMF	Fragment size	Geographic group
Mainland			
12	<0.0001	0.0027	<0.0001
51	0.0028	0.9407	0.3979
53	<0.0001	0.1422	<0.0001
Medium island			
12	0.9999	0.9959	0.0847
51	<0.0001	<0.0001	<0.0001
53	<0.0001	<0.0001	<0.0001
Small island			
12	<0.0001	<0.0001	<0.0001
51	<0.0001	<0.0001	<0.0001
53	0.8534	0.9999	0.6784

significantly higher AMF community similarity than "global AMF similarity" for two of the three forest-fragment sizes (Fig 3b; Table 2). Conversely, AMF similarities of sampling points located within plots of the same geographical group were no higher than "global AMF similarity" for two of the three geographic groups. This pattern was stronger after the removal of the outlier plot, 12 M; similarity within each forest-fragment size was significantly higher than "global AMF similarity", whereas similarity within each geographic group was no higher than "global AMF similarity" (Fig. 3b; Table 2).

AMF community similarity and distance within a 9× 9-m plot

Little spatial structure in AMF community composition was detected within each study plot. When only AMF species identity was considered (i.e., Jaccard similarity), only plot 12SI had significantly-higher AMF similarities among sampling points within 3 m, and AMF community similarity did not decay with distance in any of the study

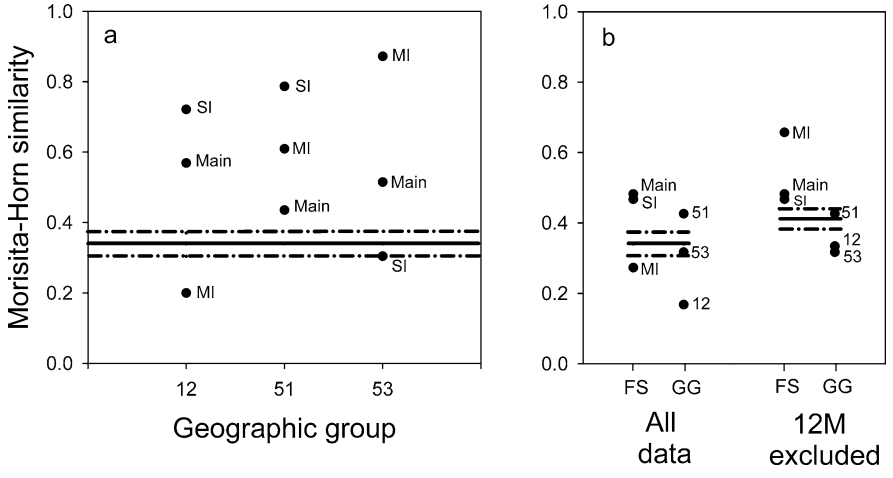

Fig. 3 **a** Mean Morisita-Horn Similarities within each of the nine plots. The *horizontal line* depicts the Global Mean AMF Similarity (mean Morisita-Horn similarity of all possible pair-wise combinations of sampling points across the nine plots). *Dotted lines* indicate standard deviation of Global Mean generated by randomization. (*Main* mainland, *MI* medium islands, *SI* small islands). **b** Mean Morisita-Horn Similarities of all possible pair-wise combinations of sampling points within each forest size (*FS*) and within each geographic group (*GG*). Similarities are presented for all data and when plot 12 M is excluded

Table 2 *P*-values indicating significance of separations of mean Morisitia-Horn Similarities of each forest-fragment size and geographic group from the "global AMF similarity" (Fig. 2b). $P \leq 0.05$ indicates a mean significantly greater than the global AMF mean

	All data	12 M excluded
Forest-fragment size		
Mainland	0.0038	0.0177
Medium islands	0.5834	<0.0001
Small islands	0.0404	0.0459
Geographic group		
12	0.9999	0.9917
51	<0.0001	0.4260
53	0.6347	0.9982

plots. Plot 53MI exhibited an increase in AMF similarity with increasing distance. When both AMF species identity and spore abundance were considered (i.e., Morisita-Horn similarity), three of the nine plots (12MI, 51MAIN, 53SI) had significantly-higher AMF similarities among sampling points within 3 m, but AMF community similarity decayed linearly with distance only in plot 53SI (Table 3).

Response of individual AMF species to fragment size and geographic location

Fifteen of the 27 AMF species or morphospecies were sufficiently abundant to be included in analysis of spore abundance. MANOVA indicated that both forest fragment size and geographic group influenced the linear combination of rank spore number of these 15 AMF species (geographic group: Wilks' Lambda=0.44, F=4.15, P=<0.0001; forest-fragment size: Wilks' Lambda=0.37, F=13.64, P=<0.0001; geographic group × forest-fragment size: Wilks' Lambda=0.53, F=2.99, P=<0.0001). Mixed-model ANOVA (each model included geographic location and its interaction as random effects) indicated that fragment size (mainland vs islands) influenced rank-spore number in five AMF species, while geographic group had an effect on spore abundance in four species (Table 4). Significant associations with fragment size by common AMF species most likely contributed to the observed pattern of community similarity. Notably, in four of the six most common AMF species, forest size significantly influenced spore abundance. Spores of *Glomus* "tsh" and *G. clavisporum* were more common in soils of mainland plots, while spores of *Glomus* "small brown" and *A. mellea* were more abundant in soils of island plots (Fig. 4).

Table 3 Results of randomization and regression analyses examining the influence of distance on AMF community similarity among sampling points within each study plot. Significant *P*-values (<0.05) derived by randomization indicate that mean similarity of sampling points within 3 m are greater than overall mean similarity of all sampling points within a plot. Significant regression coefficients ($P \leq 0.05$; marked by an *asterisk*) indicate a linear relationship between distance between sampling points and AMF community similarity (sign indicates slope direction)

	Jaccard similarity			Morisita-Horn similarity		
	Randomization	Regression		Randomization	Regression	
	P	ß	R^2	*P*	ß	R^2
12Main	0.1527	+	0.322	0.7913	+	0.338
12MI	0.5300	+	0.226	**0.0230**	−	0.157
12SI	**0.0433**	−	0.003	0.0958	−	0.137
51Main	0.4568	−	0.397	**0.0217**	−	0.443
51MI	0.2844	+	0.075	0.2610	+	0.074
51SI	0.0584	−	0.047	0.5419	+	0.043
53Main	0.7788	−	0.058	0.0772	−	0.340
53MI	0.4621	+	**0.580***	0.2720	−	0.035
53SI	0.9353	−	0.047	**0.0393**	−	**0.567***

Influence of soil characteristics and vegetation on AMF

Rank spore abundance of no common AMF species that were associated with either forest-fragment size or geographic group varied in any obvious way with soil chemistry (Tables 4, 5). However, three AMF species not influenced by geographic group or forest-fragment size were associated with soil nutrients. Rank spore abundance of *A. morrowiae* was negatively correlated with aluminum and positively correlated with soil nitrogen. Rank spore abundance of *A. scrobicualata* and *Glomus* "7" were correlated with both aluminum and calcium (Table 5). AMF species richness was negatively correlated with aluminum and positively correlated with NH_4, total soil nitrogen, and calcium.

Table 4 *F*-ratios of separate mixed-model ANOVAs that examined the influence of geographic group and forest-fragment size on rank spore numbers. Both geographic group and its interaction with forest-fragment were included as random factors

	Location	Forest-fragment size	Location× size
A. foveata	0.20	3.01	4.23*
A. mellea	17.38*	19.80*	0.68
A. morrowiae	1.88	1.24	3.96*
A. scrobiculata	0.08	0.86	3.74*
A. tuberculata	0.10	0.07	11.47*
Glomus clavisporum	0.75	76.19*	0.50
Gl. "7"	0.07	0.36	20.87*
Gl. "8"	4.99	4.01	1.51
Gl "brown"	2.04	4.69	1.52
Gl. "cluster(small)"	67.97*	60.91*	0.05
Gl. "cluster(sporocarp)"	31.28*	2.50	0.41
Gl. "red in meltz"	33.38*	5.47	0.11
Gl. "small brown"	1.54	10.81**	1.82
Gl. "tsh"	1.58	42.00*	1.82
Scutellospora calospora	1.33	0.39	1.91

*P<0.05; **P=0.08

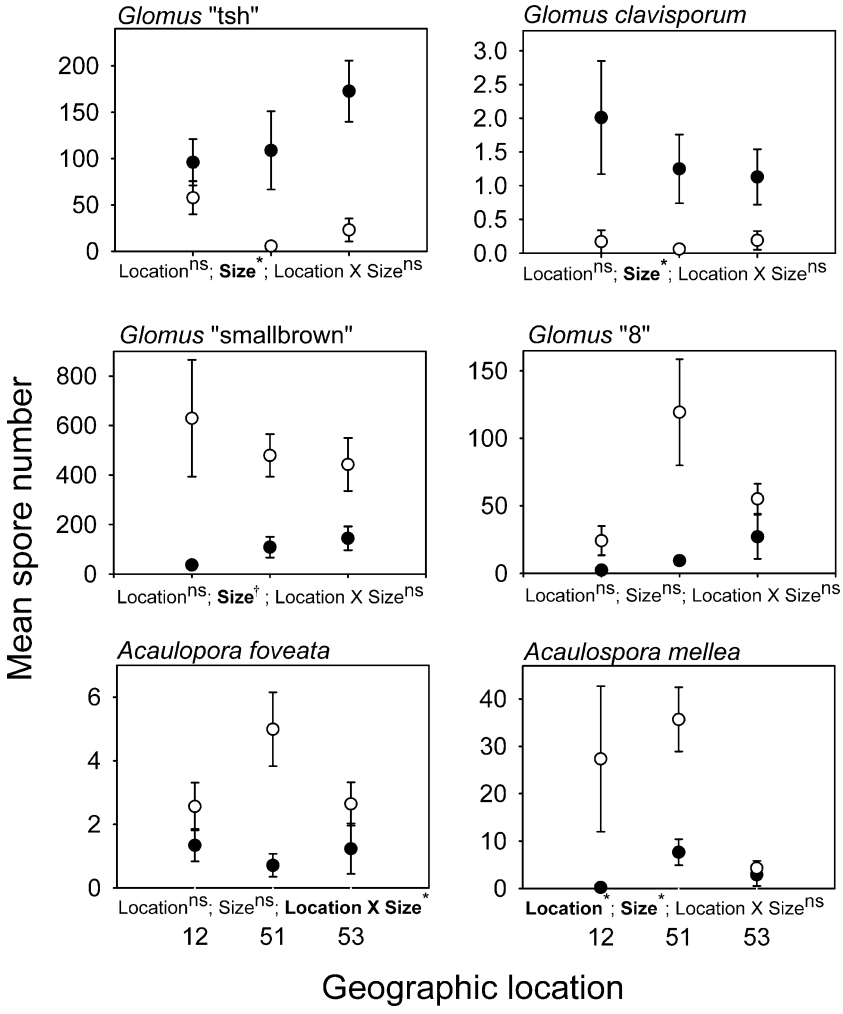

Fig. 4 Mean spore number (per 5-g dried soil) of the six most abundant AMF species for each geographic region and forest size. Each *closed circle* indicates the mean of samples (n=16) collected on mainland sites, and each *open circle* indicates the mean of samples (n=32) collected on islands

Arbuscular mycorrhizal fungal species richness was correlated negatively with Fisher's diversity of trees ≥10 cm DBH (Tables 5, 6). AMF Shannon species diversity or total spore volume was not correlated with any of the plant diversity measures (Table 5). Species richness and Fisher's diversity of both trees ≥10-cm DBH and all stems ≥0.5 m in height within each plot were negatively correlated with calcium and soil nitrogen (Table 5).

Although percent soil moisture differed significantly among the study plots, soil moisture did not consistently differ among the forest-fragment sizes and only marginally among geographic groups (forest-fragment size: F=2.575, P=0.191; geographic group: F=4.831, P=<0.086; forest-fragment size × geographic group: F=12.955, P=<0.001). *Glomus* "8" and *Glomus* "cluster(sporocarp)" were negatively correlated with soil moisture.

Discussion

In this study, we assessed how AMF spore communities were assembled in soils of intact forest and forest fragments. Although little evidence for spatial structure within each plot was detected, clear changes in AMF spore composition were found when compared across our 9×9-m study plots. Insular forests had similar AMF communities. Likewise, mainland forests had similar AMF communities, which differed from those on islands. Such community differentiation was largely explained by changes in relative abundances of spores and not solely by changes in species identity. Although several studies suggest that conversion of forest to earlier successional plant communities leads to shifts in AMF community composition, to the best of our knowledge, this is the first study to report that AMF community divergence also may occur following forest fragmentation.

AMF spore community composition

Previous studies that examined the distribution of spores in both temperate and tropical soils have clearly demonstrated that AMF species are not randomly distributed over space or time. For example, temperate surveys have identified shifts along nutrient and soil-moisture gradients (Johnson et al. 1992; Anderson et al. 1984), and different AMF species sporulated at different times of the year (Pringle and Bever 2002). Spores of tropical AMF are

Table 5 Spearman rank correlations among nutrient, AMF, and plant variables of the nine sites

	Soil moisture	Al	Ca	P	NH_4	$N0_3$	Tot N	Plant species richness	Plant Fisher's alpha	Tree species richness	Tree Fisher's alpha
AMF Richness	NS	−0.794*	0.828**	NS	0.690*	NS	0.690*	NS	−0.670*	NS	NS
AMF Shannon H'	NS	NS	NS	NS	NS	0.898**	NS	NS	NS	NS	NS
AMF spore volume	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
A. foveata	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
A. mellea	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
A. morrowiae	NS	−0.833**	NS	NS	0.750*	NS	0.683*	NS	NS	NS	NS
A. scrobiculata	NS	−0.736*	0.787*	NS	NS	NS	NS	NS	NS	−0.773*	−0.753*
A. tuberculata	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Gl. clavisporum	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Gl. "7"	NS	0.898**	−0.831**	NS	NS	NS	NS	NS	NS	NS	NS
Gl. "8"	−0.683*	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Gl. "brown"	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Gl. "cluster(small)"	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Gl. "cluster(sporocarp)"	−0.717*	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Gl. "red in melter"	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Gl. "small brown"	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Gl. "tsh"	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Scutellospora calospora	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Plant species richness	NS	NS	NS	NS	0.750*	NS	−0.950***	–	–	–	–
Plant Fisher's alpha	NS	NS	NS	NS	−0.700*	NS	−0.917***	–	–	–	–
Tree species richness	NS	NS	−0.720*	NS	NS	NS	−0.762*	–	–	–	–
Tree Fisher's alpha	NS	−0.667*	−0.850**	NS	−0.733*	NS	−0.883**	–	–	–	–

*$P \leq 0.05$; **$P \leq 0.01$; ***$P \leq 0.001$

dependent on season, soil type, nutrients, and spatial distribution of host species (Louis and Lim 1987; Harinikumar and Bagyaraj 1988; Johnson and Wedin 1997; Allen et al. 1998; Lovelock et al. 2003; Eom et al. submitted). However, few studies (especially in tropical forests) have been designed to determine the scales of change in AMF community composition in the absence of well-defined abiotic or biotic gradients.

As in all studies that estimate AMF communities based on spores, an important caveat to the interpretation of our data is how well spore abundance reflected species identities and abundances of AMF colonizing roots. The onetime sampling conducted in this study most likely underestimated true AMF-species richness of our plots because of the seasonal nature of AMF (Louis and Lim 1987; Harinikumar and Bagyaraj 1988; Pringle and Bever

Table 6 Species richness and diversity of AMF and vegetation comprising the study system. Total species richness and Shannon diversity were computed by pooling spore data from the 16 sampling points of each plot. Mean AMF species richness was computed by averaging richness of each sampling point per plot (standard deviation is in *parentheses*). Tree diversity (≥10 cm DBH) was computed for 30×30 m area surrounding each sampling plot. Diversity was computed for all stems 0.5 m in height located within each 9×9 m sampling grid

Forest size	Geographic area	AMF spore community			Trees ≥10 cm DBH within each 30×30-m plot		All plants within each 9×9-m plot	
		Species richness	Shannon H'	Mean AMF species richness per sampling point	Species richness	Fisher's Alpha	Species richness	Fisher's Alpha
Main land	12	15	1.45	4.93 (1.57)	20	14.55	45	21.24
	51	17	1.66	5.38 (1.67)	25	24.02	87	25.75
	53	16	1.69	5.06 (1.98)	26	20.20	46	17.96
Medium island	12	21	1.87	5.31 (2.12)	16	6.72	18	5.43
	51	16	2.02	5.87 (1.88)	16	9.05	35	11.49
	53	16	2.02	6.89 (1.88)	23	29.19	59	24.37
Small island	12	18	1.91	5.63 (1.50)	8	2.75	22	6.06
	51	18	1.90	5.86 (1.63)	17	7.21	34	10.64
	53	18	2.02	5.00 (1.54)	11	4.10	43	11.90

2002), and detectable species richness will no doubt increase with longer-term sampling (Bever et al. 2001). However, our sampling was conducted uniformly across sites, and any biases should occur equally across all plots. Furthermore, sampling was conducted during the rainy season, a time when spore inoculum may be important for survival of establishing tree seedlings (Garwood 1983). Consequently, the distribution of spore communities presented in this study and the suggested outcomes of such distributions are particularly relevant to forest regeneration of our study site.

In our study, evidence that forest fragmentation may promote habitat-dependent divergence of AMF spore communities emerged when we pooled sampling points (separately for each plot) and compared Morisita-Horn similarity of AMF communities across plots. Surprisingly, plots did not cluster based on geographic location (i.e., physical proximity). Instead, despite separation by more than 5 km, an AMF community located in soils of a mainland site was more similar to other mainland sites than it was to AMF communities located in soils of island plots in close proximity. Likewise, with the exception of plot 12MI, an island site was more similar to other island sites than to adjacent mainland. Also, sampling points contained within a single forest-fragment size were more similar than sampling points contained within a single geographic group, after the exclusion of the outlier, 12MI. Therefore, habitat-dependent differentiation of AMF communities occurred at both the level of the whole plot (all 16 sampling points pooled) and at the level of a single sampling point. It is unlikely that differences in the underlying geology between island and mainland sites (and not forest fragmentation per se) resulted in the observed differences in AMF communities. Plots were located at similar elevation and did not differ drastically in topography. There was no evidence for consistent differences in soil moisture between mainland and island sites during the time of sampling, nor did different parent material influence nutrient availability in the upper 15-cm soil layer of Barro Colorado Island (Yavitt 2000).

Changes in AMF spore communities were also scale dependent. Not surprisingly, AMF communities at sampling points within a 9×9-m plot were more similar to each other than to AMF communities at sampling points separated by greater distances. Interestingly, however, sampling points within two plots (12MI and 53SI) exhibited lower mean similarity than the overall "global AMF similarity" of our study area. The medium-sized island in geographic group 12 had the greatest variation across sampling points and had the highest species richness (21 species; Table 6). Consequently, mean similarity of 12MI was half that of our estimate of "global AMF similarity". However, high AMF species turnover in plot 12MI was not correlated with high turnover in vegetation. In fact, this plot had the lowest plant species richness, with bamboo (*Chusquea simpliciflora*) found throughout the plot. High dominance of this grass most likely contributed to the high species richness and notable differences in composition of AMF spores. Elevated fine-root density of grass and herbaceous vegetation resulting in higher mycelium production and sporulation may explain why AMF species richness often does not decay in pastures following forest destruction (Fischer et al. 1994; Picone 2000). Perhaps bamboo similarly resulted in the prolific sporulation of a wider range of AMF species, including those species that may rarely sporulate when hosted by woody vegetation.

At scales <100 m^2 , little evidence was found for spatial structure of AMF spore communities, thus suggesting that mechanisms that controlled local community assemblage may have operated at scales larger than our sampling plots. If vegetation type is the chief determinant of AMF spore communities as suggested by several authors (Bever et al. 1996; Eom et al. 2000; Lovelock et al. 2003), then individual trees with root systems sufficiently expansive to occupy the majority of soil within a plot may have been more important to the input of spores to the AMF community than smaller seedlings at our study site. Indeed, each plot had several common AMF species found at almost all sampling points (Appendix). Spores of common AMF species would be expected to be more heterogeneously distributed if plants with less expansive root systems were the primary source of spore input, especially considering the high species richness of vegetation (with seedlings and saplings mostly composing the plant community) found in each 9×9-m plot. Therefore, failure to detect obvious small-scale spatial structure of AMF spores at our study site, as evident in temperate grasslands (Bever et al. 1996; Pringle and Bever 2002), might have been a result of a greater divergence of size classes of root systems inhabiting our plots, with larger size classes contributing more to the spore community.

In summary, although we found little evidence for spatial structure of AMF spore communities at scales <100 m^2, such structure was clearly present at larger scales. Furthermore, changes in AMF community composition were habitat-dependent. The convergence of AMF communities on islands and convergence of mainland AMF communities (at both the whole-plot level and the sampling point level), regardless of geographic location, suggest that forest fragmentation may have promoted shifts in community composition of AMF spores. Follow-up studies are required to examine a wider range of both mainland and fragmented sites to determine the robustness of this pattern.

Underlying patterns of AMF spore community divergence

Habitat-dependent divergence of AMF communities was explained largely by shifts in relative abundance of spores of common AMF species rather than by changes in species identity (presence and absence). Although common species were found in almost all plots, spore numbers of a particular AMF species differed markedly depending on whether soils were collected from island or mainland sites. For example, spores of *Glomus* "tsh" were more abundant

in mainland soils; not only was mean spore number consistently highest on mainland plots, but this species was found in almost all of the 16 sampling points within each mainland plot and was absent at most island sampling points (Appendix). The converse was true for *Glomus* "small brown", which was a prolific sporulator on islands, but spores were less common in mainland soils. Our results are in agreement with the study by Lovelock et al. (2003), which also identified the importance of relative abundance of spores in explaining AMF community divergence in a Costa Rican forest. In that study, spores of common AMF species were associated with all of their targeted tree species, but spore numbers of an AMF species differed markedly depending on which tree species was sampled.

AMF species richness

We have found that relative abundances of common AMF species varied greatly and consistently between mainland and island sites. Nonetheless, we found little differences in the number of AMF species across these sites. The lack of decay in AMF species richness on the islands compared to the mainland contrasts with numerous studies across a wide range of plant and animal taxa in which the general rule is negative correlations between species richness and island size (MacArthur and Wilson 1967). However, this more generally observed pattern held with plant species richness, especially for trees ≥10-cm DBH (Table 6). Although there was relatively little variation in total AMF species richness across sites, the variation that did occur correlated positively with total nitrogen (primarily NH_4) and calcium, while richness and diversity of both trees ≥10-cm DBH and all stems found in each plot were strongly negatively correlated with total nitrogen (again, primarily NH_4, Table 5).

The lack of decay in species richness is consistent with several studies that have failed to detect decreased AMF-species richness of spores in soils of neotropical pastures and plantations when compared to forest soils (Johnson and Wedin 1997; Picone 2000). In light of these studies, it may be no surprise that we did not detect a decrease in AMF species richness of spores in soils of our island plots because the magnitude of decay in species richness of trees from mainland to small islands was not as large as the decay in richness following the conversion of forest to pasture. However, in both our study and in the above-mentioned studies, species richness of AMF associated with roots was unknown. If the pattern of species richness of AMF spores across study sites reflects actual species richness of AMF communities colonizing roots (i.e., any biases that occurred were consistent across mainland and island sites), then AMF defied the long-standing central tenet of island biogeography at scales in which we sampled.

Implications of AMF community divergence of spores

Our data provide solid evidence that spore communities that are available to colonize newly-emerging seedlings differ between island and mainland sites. Regardless of the primary determinant of the observed pattern of habitat-dependent spore production within an AMF species, we suggest that elevated inoculum potential caused by high numbers of spores of specific AMF species feeds back into the regenerating seedling community. Therefore, seedlings recruiting in mainland plots will have a higher probability of becoming colonized by a different suite of AMF than seedlings recruiting on islands. Such habitat-dependent differences in inoculum potential of specific AMF species may have significant consequences for seedling survival and growth, especially considering the numerous observations that different AMF species often have different growth effects on a single plant species (Mosse 1972; Bever 2002; Klironomos 2003; Eom et al. submitted).

Small islands of Gatun Lake, Panama commonly support a predictable subset of the surrounding forest's tree community, with this subset primarily composed of early successional species (Leigh et al. 1993; Adler 2000). It has been hypothesized that the selection for this subset of species is a result of altered microclimate and mammal communities following forest isolation (Leigh et al. 1993; Asquith et al. 1997). Could shifts in spore numbers of dominant AMF species help facilitate the decay in tree species composition on small forest fragments of our study system? Herrera et al. (1997) suggest that the selection of less beneficial AMF species occurs following the conversion of successionally mature plant communities to younger communities. Indeed, less beneficial AMF fungi often dominate in agricultural systems (Johnson 1993). Whether dominant AMF species found in soils of islands (e.g., *Glomus* "small brown") are less beneficial to older-growth tree seedlings, thereby limiting recruitment of certain tree species on islands is unknown and should be examined.

To conclude, the AMF spore community of our study site exhibited spatial structure across sampling plots. Species identity of the most abundant spores differed depending on whether soils were collect from islands or mainland. Such differentiation of AMF communities could have important implications for soil feedback and the composition of the regenerating tree community. If different AMF community composition is indeed due to forest fragmentation, and such changes also occur in other fragmented systems, then the consequences of habitat fragmentation for soil feedback mechanisms may contribute to shifts in composition of both aboveground plant and animal communities found around the globe following habitat alteration.

Table 7 Relative abundance and frequency of occurrence for each AMF species or morphospecies

AMF type	Relative abundance (spore volume)	Frequency of occurrence								
		12			51			53		
		Mainland	Medium island	Small island	Mainland	Medium island	Small island	Mainland	Medium island	Small island
A. foveata	7.50	8	5	10	4	11	15	5	12	2
A. mellea	7.21	2	2	13	9	15	8	3	10	2
A. morrowiae	0.34	3	10	7	3	0	2	0	2	4
A. rehmii	0.04	0	2	0	0	2	1	0	0	1
A. scrobiculata	0.33	2	7	3	4	2	1	0	0	9
A. tuberculata	5.73	2	3	1	6	2	0	0	4	10
A. "sp"	0.04	2	0	1	2	0	2	1	0	1
A. "yellow"	0.01	0	4	0	0	0	1	0	1	0
G. clarum	0.13	0	0	4	0	0	0	0	0	0
Gl. clavisporum	7.34	8	0	1	6	0	1	6	1	1
Gl. geosporum	5.16	0	9	2	0	3	0	1	0	5
Gl. rubiforme	0.01	0	0	0	0	0	0	1	0	1
Gl. sinuosum	2.06	0	6	0	0	2	0	0	0	0
Gl. "3"	<0.00	0	0	0	2	0	0	0	0	0
Gl. "4"	0.01	1	1	1	0	0	0	0	0	0
Gl. "7"	2.11	13	0	0	2	10	3	8	11	0
Gl. "8"	8.28	7	3	5	9	6	15	9	11	12
Gl. "brown"	3.70	5	6	7	2	9	7	7	10	8
Gl. "cluster(small)"	0.08	1	5	0	0	2	1	3	8	2
Gl. "cluster(sporocarp)"	1.16	2	1	1	11	4	11	5	5	4
Gl. "red in melzer"	0.11	0	2	0	3	2	6	3	6	0
Gl. "smallbrown"	18.75	8	4	15	8	14	15	9	15	10
Gl. "thin (innerwall)"	0.66	0	7	0	0	0	0	0	0	0
Gl. "tsh"	19.24	15	1	9	12	2	2	14	3	2
Gl. "white"	0.20	0	4	2	2	0	0	0	2	0
Sclerocystis coremioides	3.03	0	1	3	0	0	1	1	0	2
Scutellospora calospora	6.78	0	2	5	1	2	2	5	2	4

Acknowledgements James D. Bever, Egbert G. Leigh Jr, Damond Kyllo, Sunshine Van Bael and two anonymous reviewers provided comments on earlier versions of this manuscript. We are indebted to Arturo Morris for identifying small plants within our study plots, and we thank the Smithsonian Tropical Research Institute (STRI) for providing research facilities. This study was supported by a STRI short-term fellowship to S.A.M. and a grant from the Andrew W. Mellon Foundation to E.A.H.

Appendix

Relative abundances are based on total spore volume (across all sites) for each species. Frequency of occurrence represents the number of the sampling points (maximum of 16 per site) in which spores of each AMF species were present in Table 7.

References

Adler GH (2000) Tropical tree diversity, forest structure and the demography of a frugivorous rodent, the spiny rat (*Proechimys semispinosus*). J Zool 250:57–74

Allen EB, Rincon E, Allen MF, Perez-Jimenez A, Huante P (1998) Disturbance and seasonal dynamics of mycorrhizae in a tropical deciduous forest in Mexico. Biotropica 30:261–274

Anderson RC, Liberta AE, Dickman LA (1984) Interaction of vascular plants and vesicular-arbuscular mycorrhizal fungi across a soil moisture-nutrient gradient. Oecologia 64:111–117

Asquith NM, Wright SJ, Clauss MJ (1997) Does mammal community composition control recruitment in Neotropical forests? Evidence from Panama. Ecology 78:941–946

Augspurger CK (1984) Seedling survival of tropical tree species: interactions of dispersal distance, light-gaps, and pathogens. Ecology 65:1705–1712

Bever JD (1994) Feedback between plants and their soil communities in an old field community. Ecology 75:1965–1977

Bever JD (2002) Negative feedback within a mutualism: host-specific growth of mycorrhizal fungi reduces plant benefit. Proc R Soc London Biol Sci 269:2595–2601

Bever JD, Morton JB, Antonovics J, Schultz PA (1996) Host-dependent sporulation and species diversity of arbuscular mycorrhizal fungi in a mown grassland. J Ecol 84:71–82

Bever JD, Schultz PA, Pringle A, Morton JB (2001) Arbuscular mycorrhizal fungi: more diverse than meets the eye, and the ecological tale of why. BioScience 51:923–931

Castelli JP, Casper BB (2003) Intraspecific AM fungal variation contributes to plant-fungal feedback in a serpentine grassland. Ecology 84:323–336

Colwell RK (1997) EstimateS: Statistical estimation of species richness and shared species from samples. Version 6. User's Guide and application published at: http://viceroy.eeb.uconn.edu/estimates

Daniels BA, Skipper HA (1982) Methods for the recovery and quantitative estimation of propagules from soil. In: Schenck NC (ed) Methods and principles of mycorrhizal research. American Phytopathological Society, St. Paul, pp 39–35

Eom AH, Hartnett DC, Wilson GWT (2000) Host plant species effects on arbuscular mycorrhizal fungal communities in tallgrass prairie. Oecologia 122:435–444

Eom AH, Kyllo D, Herre EA Nonrandom associations of arbuscular mycorrhizal fungi with different host trees in a tropical moist forest: implications for community composition. (submitted)

Fischer CR, Janos DP, Perry DA, Linderman RG, Sollins P (1994) Mycorrhiza inoculum potentials in tropical secondary succession. Biotropica 26:369–377

Gange AC, Brown VK, Sinclair GS (1993) Vesicular–arbuscular mycorrhizal fungi: a determinant of plant community structure in early succession. Funct Ecol 7:616–622

Garwood NC (1983) Seed germination in a season tropical forest in Panama: a community study. Ecol Monogr 53:159–181

Gerdemann JW, Trappe JM (1974) The Endogonaceae in the Pacific Northwest. Mycol Mem 5:1–76

Gilbert GS, Hubbell SP, Foster RB (1994) Density and distance-to-adult effects of a canker disease of trees in a moist tropical forest. Oecologia 98:100–108

Harms KE, Wright SJ, Calderón O, Hernández A, Herre AE (2000) Pervasive density–dependent recruitment enhances seedling diversity in a tropical forest. Nature 404:493–495

Hart MM, Reader RJ (2002) Taxonomic basis for variation in the colonization strategy of arbuscular mycorrhizal fungi. New Phytol 153:335–344

Hartnett DC, Wilson GWT (1999) Mycorrhizae influence plant community structure and diversity in tallgrass prairie. Ecology 80:1187–1195

Harinikumar KM, Bagyaraj DJ (1988) The effect of season on a VA mycorrhizae of Leucaena and Mango in a semi-arid tropic. Arid Soil Res Rehabil 2:139–143

Helgason T, Merryweather JW, Denison J, Wilson P, Young JPW, Fitter AH (2002) Selectivity and functional diversity in arbuscular mycorrhizas of co-occurring fungi and plants from a temperate deciduous woodland. J Ecol 90:371–384

Herrera, RA, Ulloa DR, Valdés-Lafont O, Priego AG, Valdés AR (1997) Ecotechnologies for the sustainable management of tropical forest diversity. Nat Resour 33:2–17

Husband R, Herre EA, Turner SL, Gallery R, Young JPW (2002) Molecular diversity of arbuscular mycorrhizal fungi and patterns of host association over time and space in a tropical forest. Mol Ecol 11:2669–2678

Janos DP (1980) Vesicular–arbuscular mycorrhizae affect lowland tropical rain forest plant growth. Ecology 61:151–162

Janos DP (1992) Heterogeneity and scale in tropical vesicular–arbuscular mycorrhiza formation. In: Read DJ, Lewis DH, Fitter AH, Alexander IJ (eds) Mycorrhizas in ecosystems. CAB International, Wallingford, pp 276–282

Janos DP, Sahley CT, Emmons LH (1995) Rodent dispersal of vesicular-arbuscular mycorrhizal fungi in Amazonian Peru. Ecology 76:1852–1858

Johnson NC (1993) Can fertilization of soil select less mutualistic mycorrhizae?. Ecol Appl 3:749–757

Johnson NC, Tilman D, Wedin D (1992) Plant and soil controls on mycorrhizal fungal communities. Ecology 73:2034–2042

Johnson NC, Wedin DA (1997) Soil carbon, nutrients, and mycorrhizae during conversion of dry tropical forest to grassland. Ecol Appl 7:171–182

Kiers ET, Lovelock CE, Krueger EL, Herre EA (2000) Differential effects of tropical arbuscular mycorrhizal fungal inocula on root colonization and tree seedling growth: implications for tropical forest diversity. Ecol Lett 3:106–113

Klironomos JN (2003) Variation in plant response to native and exotic arbuscular mycorrhizal fungi. Ecology 84:2292–2301

Lambers JHR, Clark JS, Beckage B (2002) Density-dependent mortality and the latitude gradient in species diversity. Nature 417:732–735

Leigh EG Jr, Wright SJ, Herre EA (1993) The decline of tree diversity on newly isolated tropical islands: a test of a null hypothesis and some implications. Evol Ecol 7:76–102

Leigh EG Jr (1999) Tropical forest ecology: a view from Barro Colorado Island. Oxford University Press, New York

Louis I, Lim G (1987) Spore density and root colonization of vesicular–arbuscular mycorrhizas in tropical soil. Trans Br Mycol Soc 88:207–212

Lovelock CE, Andersen K, Morton JB (2003) Arbuscular mycorrhizal communities in tropical forests are affected by host tree species and environment. Oecologia 135:268–279

MacArthur R, Wilson EO (1967) The theory of island biogeography. Princeton University Press, Princeton

Mangan SA, Adler GH (2002) Seasonal dispersal of arbuscular mycorrhizal fungi by spiny rats in a neotropical forest. Oecologia 131:587–597

Mills KM, Bever JD (1998) Maintenance of diversity within plant communities: soil pathogens as agents of feedback. Ecology 79:1595–1601

Mosse B (1972) Effects of different *Endogone* strains on the growth of*Paspalum notatum*. Nature 239:221–223

Nemec S (1978) Response of six citrus rootstocks to three species of *Glomus*, a mycorrhizal fungus. Proc Fla State Hortic Soc 91:10–14

Olff H, Hoorens B, de Goede RGM, van der Putten WH, Gleichman JM (2000) Small-scale shifting mosaics of two dominant grassland species: the possible role of soil-borne pathogens. Oecologia 125:45–54

Packer A, Clay K (2000) Soil pathogens and spatial patterns of seedling mortality in a temperate tree. Nature 404:278–281

Picone C (2000) Diversity and abundance of arbuscular-mycorrhizal fungus spores in tropical forest and pasture. Biotropica 32:734–750

Pringle A, Bever JD (2002) Divergent phenologies may facilitate the coexistence of arbuscular mycorrhizal fungi in a North Carolina grassland. Am J Bot 89:1439–1446

Reynolds HL, Packer A, Bever JD, Clay K (2003) Grassroots ecology: plant-microbe-soil interactions as drivers of plant community structure and dynamics. Ecology 84:2281–2291

Sanders IR, Fitter AH (1992) Evidence for differential responses between host-fungus combinations of vesicular-arbuscular mycorrhizas from a grassland. Mycol Res 96:415–419

Sanders IR, Koide RT (1994) Nutrient acquisition and community structure in co-occurring mycotrophic and non-mycotrophic old-field annuals. Funct Ecol 8:77–84

SAS (1996) The SAS System for Windows, Version 6.11. SAS Institute, Cary

Schenck NC, Smith GS (1982) Responses of six species of vesicular-arbuscular mycorrhizal fungi and their effects on soybean at four soil temperatures. New Phytol 92:193–201

Siqueira JO, Carneiro MAC, Curi N, da Silva Rosado SC, Davide AC (1998) Mycorrhizal colonization and mycotrophic growth of native woody species as related to successional groups in Southeastern Brazil. For Ecol Manage 107:241–252

Streitwolf-Engel R, Boller T, Wiemken A, Sanders IR (1997) Clonal growth traits of two *Prunella* species are determined by cooccurring arbuscular mycorrhizal fungi from a calcareous grassland. J Ecol 85:181–191

van der Heijden MGA, Klironomos JN, Ursic M, Moutoglis P, Streitwolf-Engel R, Boller T, Wiemken A, Sanders IR (1998a) Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. Nature 396:69–72

van der Heijden MGA, Boller T, Wiemken A, Sanders IR (1998b) Different arbuscular mycorrhizal fungal species are potential determinants of plant community structure. Ecology 79:2082–2091

Van der Putten WH, Vet LEM, Harvey JA, Wäckers FL (2001) Linking above- and belowground multitrophic interactions of plants, herbivores, pathogens, and their antagonists. Trends Ecol Evol 16:547–554

Wills C, Condit R, Foster RB, Hubbell SP (1997) Strong density- and diversity-related effects help to maintain tree species diversity in a neotropical forest. Proc Natl Acad Sci USA 94:1252–1257

Windsor DM (1990) Climate and moisture variability in a tropical forest: long-term records from Barro Colorado Island, Panama. Smithson Contrib Earth Sci 29:1–14

Yavitt JB (2000) Nutrient dynamics of soil derived from different parent material on Barro Colorado Island, Panama. Biotropica 32:198–207

Zangaro W, Nisizaki SMA, Domingos JCB, Nakano EM (2003) Mycorrhizal response and successional status in 80 woody species from south Brazil. J Trop Ecol 19:315–324